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Coordination in parental effort decreases with age in a long-lived seabird

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Biparental care is widespread in avian species. Individuals may match the contribution of their partner, resulting in equal parental effort, or may exploit their partner, to minimise their own investment. These two hypotheses have received much theoretical and empirical attention in short-lived species, that change mates between seasons. However, in species with persistent pair bonds, where divorce is rare and costly, selective pressures are different, as partners share the value of future reproduction. In such species, coordination has been suggested to be adaptive and to increase early in life, as a consequence of the importance of mate familiarity. However, as birds age, an increase in re-pairing probability occurs in parallel to a decline in their survival probability. At the point when partners no longer share future reproductive success, exploitation of a partner could become adaptive, reducing selection for coordinated effort. As such, we suggest that coordination in parental effort will decline with age in long-lived species. Using incubation bout duration data, estimated from salt-water immersion biologgers, deployed on black-browed albatrosses *Thalassarche melanophrys*, we examined the correlation in incubation bout durations for sequential bouts, as a measure of coordination. Our results show that coordination is highest in inexperienced pairs (early in reproductive life) and declines throughout the lifetime of birds. This suggests that both cooperation, indicated by coordinated effort, and conflict over care occurs in this species. We find no change in individual bout duration with increasing breeding experience, and hence no support for the hypothesis that aging leads to changes in individual incubation behaviour. This is, to our knowledge, the first study to demonstrate strong coordination in parental care when pairs share future reproductive success, but a decline in coordination with age, as sexual conflict increases.

Keywords: albatrosses, biologging, foraging bout, incubation shift duration, life history tradeoffs, parental care, sexual conflict


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Introduction

Bi-parental care is widespread in birds, where it occurs in over 80% of species (Cockburn 2006). It is thought to be most prevalent in species where a single parent

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cannot raise offspring alone (Cockburn 2006). However, while both partners may provide care for offspring, the division of labour within the pair can be highly variable. Partners may cooperate and share the costs of rearing offspring equally (Hinde 2006, Hinde and Kilner 2007, Meade et al. 2011), or one individual may try to minimise their investment at the cost of their partner ('sexual conflict' hypothesis; Trivers 1972, Chase 1980, Houston and Davies 1985, Westneat and Sargent 1996).

In short-lived species, where divorce between breeding attempts is the predominant strategy, theoretical and empirical evidence suggest that both cooperation and conflict over care may emerge (Johnstone and Hinde 2006, Lessells and McNamara 2012). In such a conflicting situation, diverting the costs of reproduction to the partner can be adaptive (Trivers 1972, Chase 1980, Houston and Davies 1985, Westneat and Sargent 1996). When divorce is commonly costly, the maintenance of pair bonds between seasons should be under selection (Bried et al. 2003). When pair bonds are maintained between breeding seasons, it has been argued that the costs of breeding for one partner, if it decreases its future investment, will decrease the fitness of both pair members the following year (Mariette and Griffith 2012). Cooperation is, therefore, predicted to be adaptive in species with persistent pair bonds, including many long-lived species (Wittenberger and Tilson 1980, Olsson 1998, Wojczulanis-Jakubas et al. 2018). Indeed, previous studies have found that coordination in parental effort, indicative of cooperation in care, is adaptive in species with inter-annual pair bonds (Weimerskirch 1995, Mariette and Griffith 2015). However, most research has focussed on the hypothesis that coordination is adaptive, and develops with pair bond duration (Brooke 1978, Cooke et al. 1981, Fowler 1995), such that coordination should increase with age. To our knowledge, no study has considered the possibility that coordination may decline with age as the probability of re-pairing increases.

Although divorce is rare in long-lived species, the likelihood of re-pairing increases with age, as the survival probability of individuals declines. During the first breeding attempts, when the probability of breeding with the same partner the next year is high, both partners share the costs of reproduction. Selection should favour cooperation over conflict, as any disproportionate increase in effort by one pair member could have very strong consequences for the pair's fitness. As the pair ages, the probability that one partner dies, independent of its reproductive effort, increases. As a result, at a later life stage, the cost of a reproduction event will not always be equally shared between two partners, and long-lived species should then experience similar selection pressures to those of short-lived species that repair between seasons. This model assumes that pair members are of a similar age, and that both sexes have the same survival probability, which is often true in long-lived species. We therefore suggest that coordination, and therefore cooperation, should decrease with age in long-lived species.

In this study, we examine these predictions by testing three hypotheses for the change in coordination over time. First,

the widely proposed hypothesis that coordination in parental effort increases with the duration of the pair bond, which suggests that this behaviour is learnt and refined over time: hereafter the 'improvement' hypothesis (Black and Hulme 1996, Black 2001). This would manifest as an increase in coordination in parental effort with age, which would potentially plateau once partners have optimum coordination. Second, based on evidence that foraging quality may decrease with age as a result of senescence (Lecomte et al. 2010, Patrick and Weimerskirch 2015), individuals may be constrained in their ability to obtain sufficient resources and hence to coordinate their effort: hereafter the 'senescence' hypothesis. The senescence hypothesis predicts that coordination will be lower at old age and this will occur because of a change in bout duration. A change in bout duration of one partner could decouple coordination. However, if both pair members show similar changes in shift duration with age, this would be detected as a change in parental effort itself at old age with no associated change in coordination. Third, the hypothesis that as individuals age, their re-pairing probability increases and so sexual conflict will reduce the adaptive benefit of coordination; 'sexual conflict hypothesis'. This can be distinguished from the 'senescence hypothesis' as pairs will exhibit a decline in coordination with age, but no change in bout duration will be observed in models of individual incubation behaviour. This hypothesis is based on evidence that survival declines with age, and as a result, re-pairing, due to the loss of a partner, increases (Fig. 1; Pardo et al. 2013).

Black-browed albatrosses *Thalassarche melanophris* are monogamous, long-lived seabirds with a very low rate of divorce (7.7% between breeding seasons; Bried et al. 2003). Instead, re-pairing is predominantly driven by death of one partner, constituting an ideal study system to test these hypotheses. Black-browed albatrosses have prolonged reproductive cycles, lasting nine months, including long periods of parental care. In particular, their long incubation period offers an ideal opportunity to assess coordinated effort independent of chick demand. The pair share incubation and one partner must always be at the nest to ensure egg protection and thermoregulation. The individual at-sea decides the duration of their foraging trip and as a result, dictates the duration of their partner's incubation bout. The amount of time a bird spends at-sea will be linked to the amount of food they can obtain and so there is a tradeoff between individual foraging trips and the partner's bout duration. While previous work has examined the effect of age on foraging trip duration, this study aims to look at the costs of reproduction i.e. the energy use lost on the nest not the energy gained at sea. Most reproductive failure in albatrosses occurs due to egg loss, often as a result of abandonment. As a result, the conflict an individual experiences is whether to remain on the nest, and endure its energetic cost, or abandon the nest and lose the egg. It is this decision we predict will be linked to age and hence we model incubation bout duration as opposed to foraging trip duration.

Incubation bouts can be very long (mean bout duration in this population 125.99 ± 63.71 h (ca 5.25 days; range

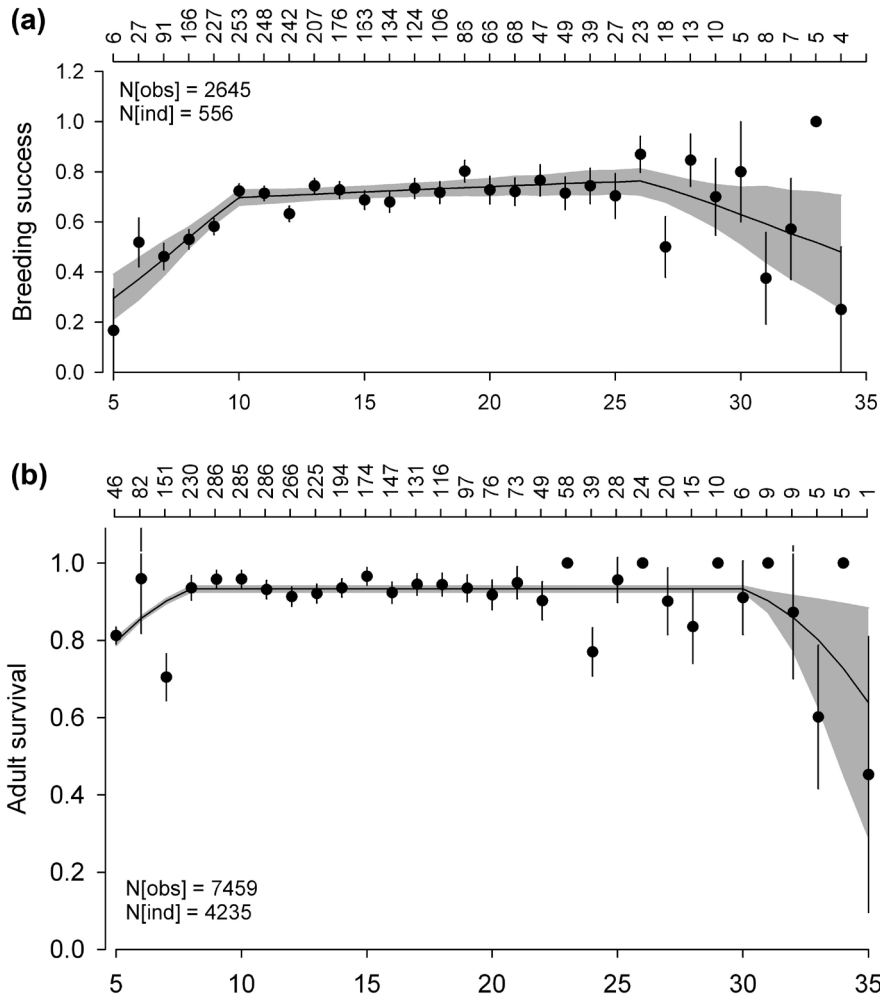


Figure 1. The relationship between age and (a) breeding success probability and (b) survival probability of black-browed albatrosses at Kerguelen (1968–2010). The solid circles correspond to the parameter estimates from a generalised linear mixed model with full age dependence and error bars are standard errors. The solid lines correspond to the best models selected using threshold models and shaded areas represent 95% confidence intervals. $n[\text{obs}]$ = total number of observations and $n[\text{ind}]$ = total number of individuals and number of observations per age are given at the top of each graph. Adapted from Pardo et al. (2013).

7.17–428.17 h). As such, birds should match their incubation bout durations if the cost of reproduction is to be carried equally to minimise costs to both birds. A mismatch will result in high mass loss for the one pair member incubating the egg, with a risk of breeding failure in the extreme case of abandonment of the nest, and insufficient time to recoup these resources and may affect both current and future reproductive success.

Material and methods

Study species and intrinsic variables

This study was conducted at Cañon de Sourcils Noirs, Kerguelen Islands (48°4'S, 68°4'E) on a population of black-browed albatrosses, which are annual breeders, with

strong monogamous pair bonds. The breeding cycle begins in October, with laying occurring in early November and chicks hatching in late December. The pair shares both incubation (period duration = 70 days) and chick brooding (period duration = 21 days) roles. They continue to provision the chick once it is left alone, until mid-April, when all chicks have fledged. Nests are checked to identify ringed individuals and birds are sexed genetically or based on the structural size of one pair member. This population has been monitored since 1979 and all adults and chicks in the study population have been ringed with a unique metal band. The population is relatively stable, with a decline of 7.8% between 1978 and 2016 (Weimerskirch et al. 2018). This stability in population size means that survival, and hence repairing will be driven by natural processes. As such, we have data on the first breeding attempt and the number of breeding attempts per individual and hence per pair, in conjunction with age and sex. Age

ranged from 5 to 35 years with a mean \pm SD of 16.62 ± 6.41 with a mean age at first breeding of 9.83 ± 2.35 .

In this study 'individual breeding experience' is defined as the number of years since an individual first bred; 'partner breeding experience' is the number of years since a bird's partner first bred. Previous studies have highlighted the issue of small sample size at the extremes of age distributions and this is particularly pertinent in studies of changes in behaviour with age in long-lived species (Froy et al. 2013, Patrick and Weimerskirch 2015). Failure to account for this can result in false quadratic relationships being detected. To control for this, groups of <5 individuals were collapsed into a single group, and given an associated age class. As a result, for individual breeding experience values >16 years, samples sizes were insufficient (17 years; $n=2$; 18 years; $n=1$; 19 years; $n=1$; 20 years; $n=1$; 21 years; $n=1$) and so were collapsed into a single class (17 years; $n=6$). Breeding experience and age are known to be strongly correlated ($r=0.86$; $p < 0.001$), and breeding experience was favoured for analyses in this study for two reasons: First, breeding experience is a more accurate representation of lifetime reproductive effort of the birds as it is independent of age at first reproduction and second, as some birds are ringed as adults, their true age is unknown but their breeding experience is accurately measured. 40% of birds recruit to our population from outside the study area and are hence ringed as adults and their age must be estimated. 60% of birds are born in the study population and ringed as chicks – this means their age at first reproduction is known exactly. We know that in this species birds are highly philopatric and do not commonly move breeding areas post-recruitment and in fact 74.4% of birds are faithful to the same nest (Bried et al. 2003). As such, we can assign breeding experience to all birds with a high degree of certainty. However, we discuss our results in the context of age as we used breeding experience as a proxy for age in this system.

While biologging studies have dramatically improved our ability to study foraging behaviour, longitudinal data is still rare, such that changes within an individual are hard to quantify. For long-lived species it may take decades to have sufficient data to capture within individual changes over a lifetime. We suggest that given these constraints, cross-sectional analyses offer the only currently available opportunity to examine age-specific effects, and provide powerful and valuable insights into foraging differences at different life-stages, and such analyses have been used extensively in long-lived species when longitudinal data is not available.

Parental effort data collection

From 2006 to 2013 adult breeding black-browed albatrosses were equipped with geolocation-immersion logger (GLS; British Antarctic Survey, Cambridge, UK; Mk4, Mk5, Mk9, Mk15, Mk19 models) and Mk3006 (Biotrack/Lotek). These loggers weighed 5 g (Mk4), 3.6 g (Mk5) or 2.5 g (other models), which is 0.0–0.14% of the adult body mass (see Desprez et al. 2018 for details). Birds were caught on the nest

and devices, attached to plastic rings, were fitted on the legs. For this study, we used data from the salt-water immersion loggers, which detect when the bird is on the water- i.e. the logger is immersed in salt water. Mk4, Mk5, Mk9, Mk15 and Mk3006 loggers record the proportion of each 10-min interval the electrodes are immersed and Mk19 record the actual duration of immersion. Data was collected over six years (2007: $n=11$; 2008: $n=5$; 2009: $n=21$; 2010: $n=69$; 2012: $n=28$). In total, 115 birds equipped with a GLS logger were included in this study, totalling 196 bird years of data. For pair analysis this was reduced to 113 birds and 193 bird years due to missing partner data on a small number of individuals. Individuals were tracked for 1–4 years and all individuals used in this study were of known sex and breeding experience. These biologging devices enabled the automated recording of incubation bout duration throughout and between breeding seasons, collecting a unique set of data.

Quantifying parental behaviour

When foraging at sea, birds alternate periods in flight (logger records = 'dry') and periods on the water ('wet', the feet and lower leg of the bird carrying the GLS is in the salt water, producing a contact between two electrodes). 'Dry' periods of <7 h are indicative of flight (maximum continuous flight time; Desprez et al. 2018). 'Dry' periods greater >7 h correspond to periods when the bird is on land. The start of the incubation bout, or period on the nest, is thus measured between the end of the last 'Wet' event before a 'Dry' period >7 h, and the following 'Wet' event is considered the end of the bout, when birds return to sea and immediately land on the water after leaving the colony. The incubation bout is the duration of this period. The incubation bout duration of one bird corresponds well to the foraging trip duration of the partner, as they spend only short periods together at the nest. These values are approximations with a maximum error of 7 h. The mean bout duration for individuals was 125.99 ± 63.71 h, and as such an error of 7 h is only 5% of the total measurement. Throughout the manuscript 'individual bout duration' is defined as the time the bird spends on the nest. 'Partner bout duration' is defined as the duration of the partner's bout immediately before that of the focal bird.

Statistical analyses

Two main models were used to examine drivers of variation in individual bout duration. First, an 'individual bout duration model' was modelled as a function of breeding experience and sex. This model was used to examine the intrinsic drivers of individual bout duration, independent of a partner's behaviour. Evidence from other albatross species suggests age and sex drive differences in individual bout duration (Lecomte et al. 2010, Patrick and Weimerskirch 2015), but these relationships are unexplored in black-browed albatrosses. Previous studies examining these effects have not taken account of the partner behaviour and so we first omitted partner behaviour when fitting the individual

bout duration model to allow direct comparison with previous work. Second, we extend this model to include partner behaviour in a 'coordination in bout duration model'. In this model, an individual's bout duration was fitted in relation to their partner's behaviour, also controlling for intrinsic effects on bout duration, to estimate the coordination in bout duration between the pair.

In the individual bout duration model, individual bout duration of the focal bird was fitted in a model with a Gaussian error structure. Individual breeding experience, sex, the interaction between individual breeding experience and sex and a binary measure of whether it was a bird's first breeding attempt were included as fixed effects in the model. Given evidence of quadratic changes in behaviour and survival with age, which differ between the sexes in albatross species (Lecomte et al. 2010, Pardo et al. 2013, Patrick and Weimerskirch 2015), we included a quadratic individual breeding experience term and the interaction between this and sex. Individual ID and year were included as random intercepts.

In the coordination in bout duration model, coordination was measured as the coefficient of the slope between the bout lengths of a pair, over sequential trips, where a strongly positive slope between partners bout durations is evidence of strong coordination and weak slope evidence of little coordination. At the population level overall, partners showed a weak positive correlation in bout duration suggesting some level of coordination (the correlation between a bird's bout duration and that of its partner the preceding trip: $r^2 = 0.11$). The individual bout duration of the focal bird was fitted in a model with a Gaussian error structure. Partner breeding experience was fitted using linear and quadratic effects. As Pardo et al. (2013) (Fig. 1) suggest that both the survival probability, and the reproductive performance, are best explained by a three-piecewise regression model, we fit a model grouping observations into inexperienced (<2 years breeding experience; average age = 12 years), medium experience (3–9 years breeding experience; average age = 17 years) and experienced

(>9 years breeding experience; average age = 22 years), using threshold values from this paper. We have insufficient data to fit a piecewise regression but our model allows the slopes to differ, and hence the coordination level, between these groups. A binary measure of change in partner was included to control for any effect of new partnerships and a binary measure of first breeding attempt was included to assess the difference in behaviour of new recruits. The average age at first breeding in this study was 9.83 years \pm 2.35 (mean \pm SD) and rearing was 20.33 years \pm 6.62 (Supplementary material Appendix 5). The difference in breeding experience between the partners was included to account for the effect of mismatched pair experience. The interaction between linear and quadratic effects of partner breeding experience and partner bout duration were fitted in models. The following interactions with partner bout duration were also fitted in both models: First breeding attempt, the difference in breeding experience between partners and new partnerships. Pair ID and year were included as random intercepts and partner bout duration as a random slope at the pair level, to allow coordination to vary at the between pair level. Final model structures can be found in Table 1, 2. Models were run in lme4 (Bates and Maechler 2010) and the significance of fixed effects was assessed by using Likelihood ratio tests (maximum likelihood) comparing models with and without the term of interest. All variables were scaled with a mean of 0 and a standard deviation of 1, and as such all estimates from models are based on scaled values. Interactions were added iteratively to the final model due to the complexities of the models and all non-significant interactions were removed from the final models.

Results

Individual bout duration

The mean individual incubation bout duration differed significantly between the sexes, with males having longer

Table 1. Intrinsic effects on individual bout duration (hours). Results for a model of individual bout duration with sex, breeding experience and first breeding attempt. All variables are scaled with a mean = 0 and standard deviation = 1 and 115 individuals were included in the final model. Non-significant interactions were dropped from models. The effects retained in the final model are shown by a ✓ and those omitted by ✗. Significant effects are shown in bold.

	Final model	Scaled parameter estimate	SE	χ^2	df	p-value
Effects on individual bout duration						
Intercept	✓	−0.28	0.19			
First time breeder	✓	−0.09	0.14	0.38	1	0.54
Sex – Male	✓	0.35	0.09	15.08	1	<0.001
Individual breeding experience	✓	−0.02	0.05	0.14	1	0.71
Individual breeding experience \times Sex	✗	−0.04	0.09	0.19	1	0.66
Individual breeding experience ²	✗	0.02	0.20	0.01	1	0.93
Individual breeding experience ² \times Sex	✗	−0.29	0.31	0.94	1	0.33
Random effects						
ID random intercept	✓	0.16				
Year random intercept	✓	0.17				
Residual variation	✓	0.75				

Table 2. Coordination between partners in bout duration, and the importance of breeding experience. Results for a model of individual bout duration with partner bout duration, sex, breeding experience, first breeding attempt, change of partner and the difference between the breeding experience of the pair. All variables are scaled with a mean=0 and standard deviation=1 and 113 individuals were included in final models. Non-significant interactions were dropped from models. The effects retained in the final model are shown by a ✓ and those omitted by ✗. Significant effects are shown in bold.

	Final model	Scaled parameter estimate	SE	χ^2	df	p-value
Effects on individual bout duration						
Intercept	✓	-0.27	0.16			
First time breeder	✓	-0.14	0.15	0.94	1	0.33
Sex – Male	✓	0.42	0.07	38.58	1	<0.001
Partner breeding experience	✓	-0.42	0.18			
Bout duration partner	✓	0.22	0.04			
Difference in breeding experience between partners	✓	0.09	0.04	4.29	1	0.04
New partner	✓	-0.13	0.10	1.67	1	0.20
Partner breeding experience ²	✓	0.35	0.16	12.17	1	<0.001
Interactions estimating effects on coordination						
First time breeder × Bout duration partner	✗	0.15	0.10	2.07	1	0.15
Partner breeding experience × Bout duration partner	✓	-0.13	0.04	11.15	1	<0.001
Difference in breeding experience between partners × Bout duration partner	✗	-0.03	0.05	0.32	1	0.57
New partner × Bout duration partner	✗	0.10	0.07	1.89	1	0.17
Partner breeding experience ² × Bout duration partner	✗	0.17	0.12	2.01	1	0.16
Random effects						
ID random intercept	✓	0.06				
ID – Bout duration partner random slope	✓	0.01				
Year random intercept	✓	0.14				
Residual variation	✓	0.71				

bouts (model estimate = 0.05 ± 0.19) than females (model estimate = -0.30 ± 0.19 ; $\chi^2_1 = 15.08$; $p < 0.001$; Table 1, Fig. 2), indicative that females have longer foraging trips. First time breeders showed no significant difference in individual bout duration compared to other birds, and there was no significant linear or quadratic effect of individual breeding experience on individual bout duration nor an interaction with sex (Table 1).

Coordination in bout duration

We detected an interaction between partner breeding experience and partner bout duration, demonstrating that coordination varies with partner breeding experience ($\chi^2_1 = 11.16$; $p < 0.001$; Table 2). Less experienced partners were more coordinated than more experienced individuals, controlling for other important parameters (Fig. 3). When individuals were grouped into inexperienced, medium experience and experienced, to allow for the level of coordination to differ between these subsets, there was a strong effect of breeding experience group ($\chi^2_2 = 13.50$; $p < 0.001$). The results mirrored that of the linear relationship with medium experience showing a moderate slope (0.15 ± 0.05 ; reference slope), inexperienced birds have a stronger level of coordination (0.33 ± 0.09), and experienced birds the lower level (-0.07 ± 0.09).

As in the previous model, males had longer bout durations than females ($\chi^2_1 = 38.58$; $p < 0.001$; Table 2). Individuals

with a larger difference in breeding experience with their partner had longer bout durations ($\chi^2_1 = 4.29$; $p = 0.04$; Table 2, Fig. 4). There was a relationship between individual bout duration and a quadratic effect of partner breeding experience,

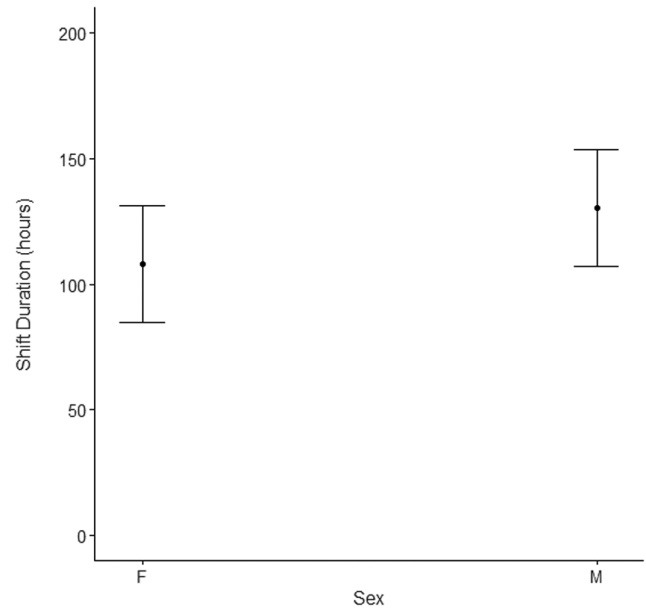


Figure 2. Sex differences in individual bout duration. Parameter estimates are extracted from a model with non-scaled variables. Females have shorter bout durations than males.

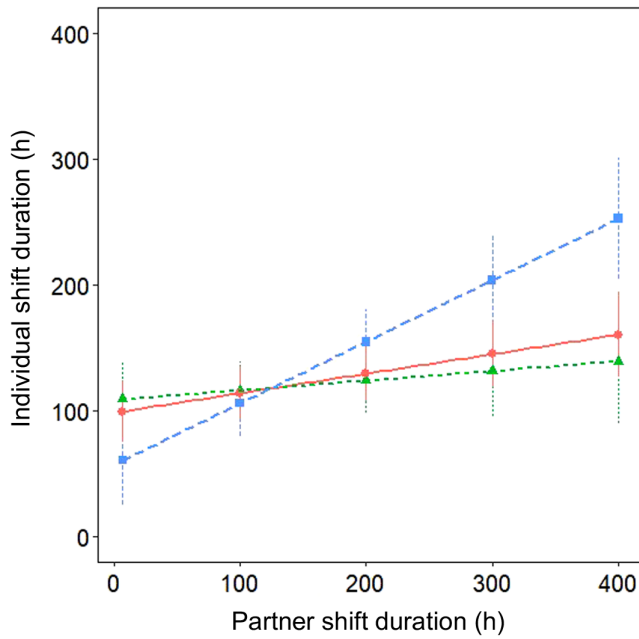


Figure 3. Breeding experience and coordination in bout duration. The linear interaction between partner breeding experience and partner bout duration on individual bout duration is shown here with partner breeding experience divided into three groups blue line=Inexperienced birds (< 3 years); red line=Medium experience (3–9 years); green line=Experienced (> 9 years). Coordination, evidenced here as the strength of the slope, is lowest for experienced birds and highest for inexperienced birds.

with a higher bout duration for inexperienced and experienced birds ($\chi^2_1 = 12.17$; $p < 0.001$; Table 2, Fig. 5), but it was not mirrored in the models of individual bout duration.

Discussion

Our results show that black-browed albatrosses, a species with long-term, inter-annual pair bonds, show coordination in incubation bout duration within a pair, and that this coordination decreases with breeding experience. We find no strong evidence of changes in individual bout duration itself with breeding experience, and hence no support for the senescence hypothesis, which predicts a change in foraging behaviour with age will change the level of coordination between partners. We also find no evidence that coordination increases with breeding experience, indicative of the improvement hypothesis, which suggests that birds learn and refine their coordination over time, and as such this increases with age. Our results therefore suggest that declines in survival, and increases in re-pairing probability with age, may increase sexual conflict and hence decrease selection for coordination in parental effort. This provides some of the first evidence that coordination in parental care declines with age, suggesting changes in sexual conflict with survival probability may drive changes in coordination in a long-lived seabird.

Coordination is thought to be adaptive in monogamous species, particularly during incubation, when the behaviour of one pair member directly influences the costs to the other. It has been suggested that time and energetic constraints are strongest during this period and coordination improves the division of labour (van de Pol et al. 2006). The correlation between mass loss on the nest and the time required to forage and replenish lost resources may result in an energetic constraint that forces coordination if body condition is to be maintained by both partners (Weimerskirch 1995). In support of this, our results show that the population generally exhibits some level of coordination. However, our study suggests that the level of coordination is lower than has been

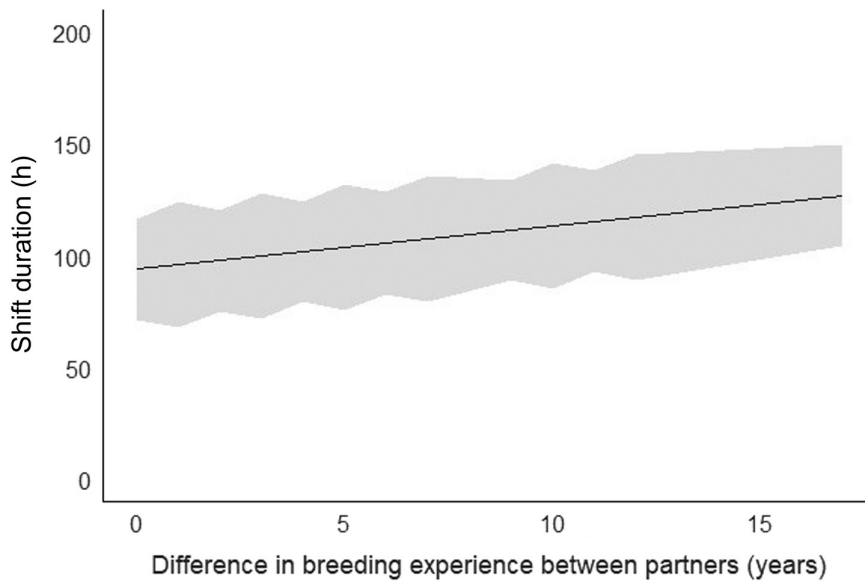


Figure 4. The relationship between the difference in the breeding experience of pairs and individual bout duration. Parameter estimates are extracted from a model without scaled variables. Birds which have more different breeding experiences have longer trips.

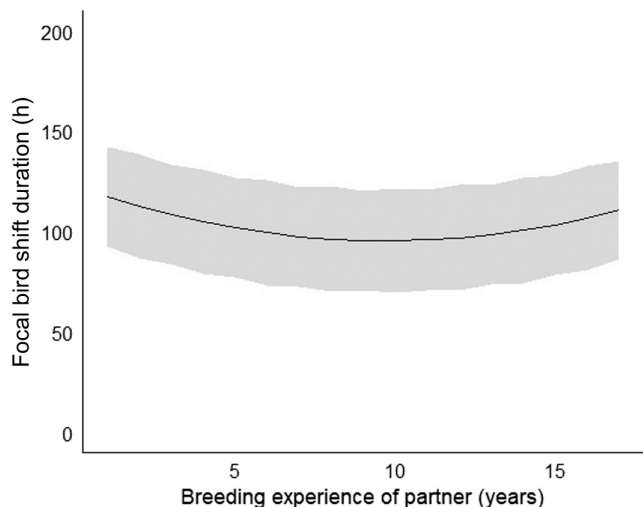


Figure 5. The quadratic relationship between the breeding experience of bird and its partner's bout duration. Parameter estimates are extracted from a model without scaled variables. There is a weak negative quadratic relationship, with individuals with inexperienced and experienced partners having longer bout durations.

previously suggested and while the drivers of an individual's foraging trip duration will likely include the trip duration of their partner, and hence the time on the nest, there may be other important effects. For example, some individuals forage more efficiently, and as a result are better able to obtain sufficient resources in a shorter time period. However, what is not known is whether these differences would lead individuals to return to the colony sooner, or simply exploit the additional time to obtain extra resources. Such decisions are likely crucial in understanding the adaptive benefit of coordination and the energetic and biological limits to pair behaviour.

In contrast to previous studies (Coulson and White 1958, Brooke 1978, Cooke et al. 1981, Fowler 1995), we find that individuals that are breeding for the first time are significantly more coordinated than experienced breeders. Our study uses a large sample size, and controls for a range of important parameters. This result is mirrored when examining how coordination changes longitudinally with breeding experience. Black-browed albatrosses have delayed recruitment and a prolonged period of mate choice pre-recruitment (Weimerskirch 1992), and recent work on other seabird species has shown a possible refinement of foraging strategies pre-recruitment (Votier et al. 2017). As a result, we suggest that birds in this population may have already developed coordination within pairs before their first breeding attempt. There is little known about the relationship between the duration of the mate choice period and foraging traits. Young albatrosses return to the colony around three years old to choose a mate. After this they can spend several seasons at the colony together before they begin breeding. While we understand this process at the population level, we know little about how individuals differ from one another, nor how this impacts on the early reproductive success or chance of divorce. However, given studies on species with much earlier

recruitment (Votier et al. 2017) have demonstrated refinement pre-breeding, in a species like albatrosses which recruit late and have a prolonged period of pair formation lasting several years, this period is likely to be crucial in developing foraging strategies, both individually and within a pair, and may be the period during which coordination develops.

Studies of sexual conflict to date have not modelled how selection acts in species with interannual pair bonds (Mariette and Griffith 2015). However, the assumptions of these models, specifically regarding the fitness benefits of the transfer of reproductive costs to a partner, can clearly be demonstrated to differ when pair bonds persist between seasons. This therefore supports our results showing strong coordination in early life, when re-pairing probability is very low. Given theory predicts sexual conflict over care should occur when pair bonds do not persist between seasons, in long-lived species, selection should act similarly once pair bonds begin to break down. Exploration of a subset of data, where birds are still breeding with their original partner, shows the same results as we present in the main manuscript with the full data set (Supplementary material Appendix 4). This provides support that it is the perceived risk of re-pairing with age that drives these results, not the act of re-pairing itself. We therefore argue that our results may demonstrate that sexual conflict in black-browed albatrosses increases in later life and that this explains the observed decline in coordination in care.

This raises questions beyond our study system as to whether the cost of re-pairing between seasons may be sufficiently large to limit the conflict between partners. To fully address this, a study comparing the level of coordination in relation to re-pairing rates and the associated changes in fitness is required, but we believe our results pave the way for this hypothesis to be tested in other systems. Models examining cooperation and conflict over care would benefit from including multiple reproductive attempts and mate fidelity to provide a better framework for empirical studies in the future. While many studies assume that coordination should be adaptive in long-lived species, the costs and benefits have not been thoroughly modelled (Mariette and Griffith 2015).

There are few predictions in the literature as to how coordination should change across the lifetime of individuals, beyond the first few years of reproduction, or indeed in species with persistent pair bonds. One prediction stems from previously reported changes in foraging behaviour with senescence in a closely related species (Lecomte et al. 2010, Patrick and Weimerskirch 2015). Such changes have been attributed to stronger individual constraints on foraging with age, which may in turn reduce an individual's ability to match their partner's effort. However, here we found little support for this hypothesis. We were unable to explore the hypothesis that individuals may experience senescence in coordination itself in this study. This would manifest as a decrease in coordination with individual age, but not partner age. If an individual became more variable in its bout duration with age, this increase in variance could act to decouple the pair coordination, while bout duration remains unchanged. We show some preliminary attempts to explore this hypothesis (Supplementary material

Appendix 3), but to robustly test this hypothesis, a system where individuals do not pair assortatively by age is needed, to allow these effects to be decoupled. Equally, it would very interesting to explore the interaction between not only age and coordination, but the effect of changing partner on this interaction. This would allow us to look at whether changes in coordination with age are driven by the increase in repairing rate, or age itself but a large amount of data on older birds would be needed for such models.

Models looking directly at changes in individual bout duration with age show no support for a quadratic change with age and hence no evidence of senescence of bout duration itself. Interestingly, in coordination models, there was some evidence of a quadratic effect of partner age on bout duration but not the coordination between partners. Further work would be needed to examine why effects that are not detectable at the individual level can be identified in partner bout duration in coordination models, and what the biological meaning of such effects are. We found that an increased difference in the age between the two pair members was coupled with longer bout durations. This relationship was weak and we found no effect of changing partner on bout duration or coordination. However, there could be an interaction between changing partner and the age of the new partner, as increases in the age difference of pairs is thought to occur due to re-pairing in later life. We were unable to model this in our study as re-pairing events are rare, as are large age differences between pair member, but this would be an interesting extension of this work. The sex differences in incubation bout, and hence foraging trip duration, found here are well documented, with strong evidence that males make shorter foraging trips, and forage nearer to the colony (Patrick and Weimerskirch 2014) and as such this may allow males to return to the colony sooner.

In conclusion, our study provides some of the first evidence that when the value of future reproduction is shared between partners, due to long-term pair bonds, selection favours coordinated parental effort during incubation. We test this hypothesis using a unique data set to compare pairs with high and low probabilities of re-pairing. We demonstrate that when the chances of breeding in the future are reduced the value of future reproduction is less likely to be shared and coordination decreases. This evidence suggests that sexual conflict is minimised while the costs of current reproduction for an individual are shared by the partner in subsequent seasons and offers an explanation for strong coordination in long-lived species. Our results highlight the importance of understanding the behaviour of both pair members in species with obligate parental care, and raises novel questions regarding the value of maintaining pair bonds and how changes in parental investment are associated future reproductive performance.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.3j9kd51g5>> (Patrick et al. 2020).

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Supplementary material (available online as Appendix oik-07404 at <www.oikosjournal.org/appendix/oik-07404>). Appendix 1–6.